

LIFE HISTORY AND DESCRIPTIONS OF IMMATURE STAGES OF
TEPHRITIS ARIZONAENSIS QUISENBERRY (DIPTERA: TEPHRITIDAE)
ON *BACCHARIS SAROTHOIDES* GRAY IN SOUTHERN CALIFORNIA

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Abstract. — *Tephritis arizonaensis* Quisenberry is bivoltine and monophagous, or nearly so, on *Baccharis sarothroides* Gray (Asteraceae). The F₁ larvae feed and develop in non-galled, branch-tip mines, the only Nearctic Tephritidae known to do so; whereas, the F₂ larvae develop singly in male or female flower heads. Eggs and ova, second and third instars, and the puparium of this tephritid are described for the first time. The discovery of a laterally striated, membraneous sheath covering each ovum is reported. The median oral lobe of second and third instars is attached to the floor of the mouth lumen, as reported to date for only one other, noncongeneric, nonfrugivorous, North American tephritid. The puparium is tightly girdled by a cylinder of host-plant epidermis inside the branch tip mine, which bears a characteristic vent hole basally. Adult behaviors, including courtship and copulation, are described. Hymenopterous parasitoids of *T. arizonaensis* include two species of solitary, primary endoparasitoids, *Pteromalus* sp. and *Dinarmus* sp. (Pteromalidae), and two species of solitary, primary, endoparasitic *Eupelmus* (Eupelmidae). This tephritid may be worth evaluating further as a candidate agent to export for the biological control of weedy *Baccharis*.

Key Words: Insecta, *Tephritis*, *Baccharis*, biology, biological weed control, gall evolution, monophagy, phytophagy, taxonomy of immature stages, mating behavior, parasitoids

Eighteen species of *Tephritis* indigenous to North America have been described (Foote 1960, Stolzhus 1977, Foote and Blanc 1979, Jenkins and Turner 1989), but the biologies of only two of these are known in great detail, i.e. *T. stigmatica* (Coquillett) on *Senecio* spp. (Tauber and Toschi 1965, Goeden 1988a) and *T. baccharis* (Coquillett) on *Baccharis salicifolia* (Ruiz and Pavon) Persoon (Goeden and Headrick 1991a). This paper describes the life history of a third Nearctic species, *T. arizonaensis* Quisenberry, on *B. sarothroides* Gray in southern California.

MATERIALS AND METHODS

Two locations in San Diego Co. in southern California were used as primary study sites: Otay Mesa overlooking San Ysidro just north of Tijuana, Mexico, at 45-m elevation, and near Loveland Reservoir, 5 km south of Alpine at 480-m elevation. Field observations on the F₁, branch-mining generation were principally made at these two locations during 1989–91. Flower heads containing F₂ larvae and puparia also were sampled at several additional locations reported below. Samples of branch mines and flower heads containing larvae and puparia

were returned to the laboratory for dissection, photography, description, and measurement. All larvae and three puparia dissected from these mines were preserved in 70% EtOH for scanning electron microscopy (SEM). All other puparia were placed in separate glass rearing vials stoppered with absorbant cotton and held in humidity chambers for adult emergence. Specimens for SEM later were rehydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia, as well as overwintered adults swept from *B. sarothroides*, were individually caged in 850-ml, clear-plastic, screened-top cages fitted with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests. Virgin male and female flies obtained from emergence vials, as well as field-collected adults, were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton (Headrick and Goeden 1991) for direct observations, videorecording, and still-photography of their general behavior, courtship, and copulation. Pairs were held together for at least 1 week, and observations were made throughout the day.

Plant names used follow Boldt (1989); tephritid names follow Jenkins and Turner (1989). Voucher specimens of *T. arizonaensis* from each study site are located in the research collection of RDG (Department of Entomology, University of California, Riverside). RDG also maintains a separate collection of hymenopterous parasitoids of California Tephritidae; DHH has

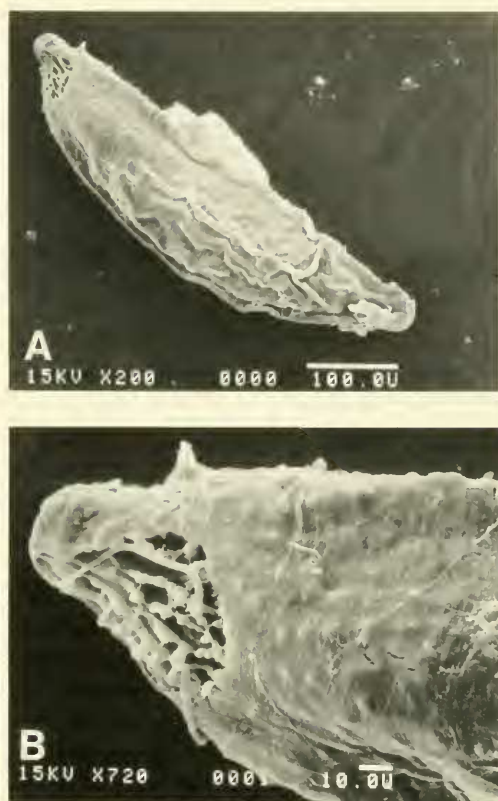


Fig. 1. Egg of *T. arizonaensis*: (A) habitus, dissected from gravid female; (B) detail of pedicel, showing membranous sheath and polygonal reticulation.

established a separate collection of immature Tephritidae. Means \pm SE are provided throughout this paper.

RESULTS AND DISCUSSION

TAXONOMY

Quisenberry (1951) described *T. arizonaensis*. In their revision of the *Baccharis*-infesting *Tephritis* species of North America, Jenkins and Turner (1989) reviewed the taxonomy, measured ova, described and illustrated the male genitalia, and described the light and dark morphs of *T. arizonaensis* adults.

Egg.—Ova white, fusiform-ellipsoidal; 16 averaged 0.64 ± 0.01 mm long, 0.28 ± 0.01 mm wide (Fig. 1A); anterior end bears a

short pedicel 0.02 mm long, 0.01 mm wide; ovum covered by a laterally striated, membranous sheath.

These means differed only slightly from means of 0.69 and 0.24 mm for lengths and widths, respectively, of five ova measured by Jenkins and Turner (1989). The eggs of *T. baccharis* (Coquillett) are very close in size to both sets of measurements (Goeden and Headrick 1991a), but both of these species have smaller ova than *T. californica* Doane and *T. rufipennis* Doane, also measured by Jenkins and Turner (1989). The ovum examined with SEM was found to be covered by a laterally striated, membranous sheath. The sheath is either partially or fully removed during oviposition thus exposing the aeropyle and polygonal reticulation. Re-examination of *T. baccharis* eggs illustrated by Goeden and Headrick (1991a) showed a similar sheath rolled back to the middle of the egg body where it entered the stem. The nature of this sheath and its function remain unclear, as it has never been described or illustrated for any other insect (Hinton 1981). The polygonal reticulation typical of *Tephritis* eggs was seen beneath this sheath in *T. arizonaensis* (Fig. 1B).

Third instar.—Third instar superficially smooth, elongate, cylindrical, tapered anteriorly and truncated posteriorly; gnathocephalon conical with many small rugose pads; anterior sensory lobes flattened, separated by a medial depression (Fig. 2A); paired dorsal sensory organs dorsad of anterior sensory lobes and consist of a single dome-shaped papilla (Fig. 2A-1); anterior sensory lobes bear lateral sensory organ (Fig. 2A-2), pit sensory organ (Fig. 2A-3), and terminal sensory organ (Fig. 2A-4); stomal sense organs lie ventrad of anterior sensory lobes, near lateral aspect of mouth lumen (Fig. 2A-5); two distinct lobes lie laterally and ventrolaterally on the gnathocephalon (Fig. 2B-3); each bears small, dome-shaped, smooth, verrucate papilla with a central pore; mouth hooks tridentate, teeth stout and bluntly conical (Fig. 2A-6, 2B-1); me-

dian oral lobe smooth ventrally, laterally flattened, attached to floor of mouth lumen (Fig. 2B-2); labial lobe bears paired sensilla (Fig. 2B-4); prothorax smooth, bearing several stelex sensilla; anterior thoracic spiracle located dorsolaterally on the posterior margin bearing three or four papillae (Fig. 2C); mesothorax, metathorax and abdominal segments superficially smooth and circumscribed by shallow, longitudinal depressions; intersegmental area bears rows of minute acanthae; lateral spiracular complex located near anterior margins of segments T-II to A-VII composed of an open lateral spiracle (Fig. 2D-1), and two dome-shaped sensilla, each with a central pore (Fig. 2D-2); caudal segment bears posterior spiracular plates; plates bear three, elongate-oval rimae ca. 0.05 mm long (Fig. 2E-1), four interspiracular processes with three to five branches each; the longest process measured 0.01 mm in length (Fig. 2E-2); stelex-type sensilla surround margin of caudal segment in four-dorsal, six-ventral arrangement; additionally, the caudal segment bears a pair of compound sensilla ventrad of the spiracular plates (Fig. 2F); each pair consists of a stelex sensillum (Fig. 2F-1), and a tuberculate, medusoid, chemosensillum resting in a shallow depression (Fig. 2F-2).

Tephritis arizonaensis is very similar to *T. baccharis* in the type of sensory structures and their placement with a few noticeable differences that may be of taxonomic importance. The rugose pads on the gnathocephalon are not dorsoventrally elongated as in *T. baccharis* (Goeden and Headrick 1991a). The lateral spiracular complex is composed of a spiracle and two dome-shaped sensilla in *T. arizonaensis*. The complex is similar to that described for *T. baccharis* (Goeden and Headrick 1991a) and *Neaspilota viridescens* Quisenberry (Goeden and Headrick 1992). However, in *T. baccharis* there are three associated, dome-shaped sensilla, and in *N. viridescens*, there is only one dome-shaped sensillum (Goeden and Headrick 1991a, 1992). The num-

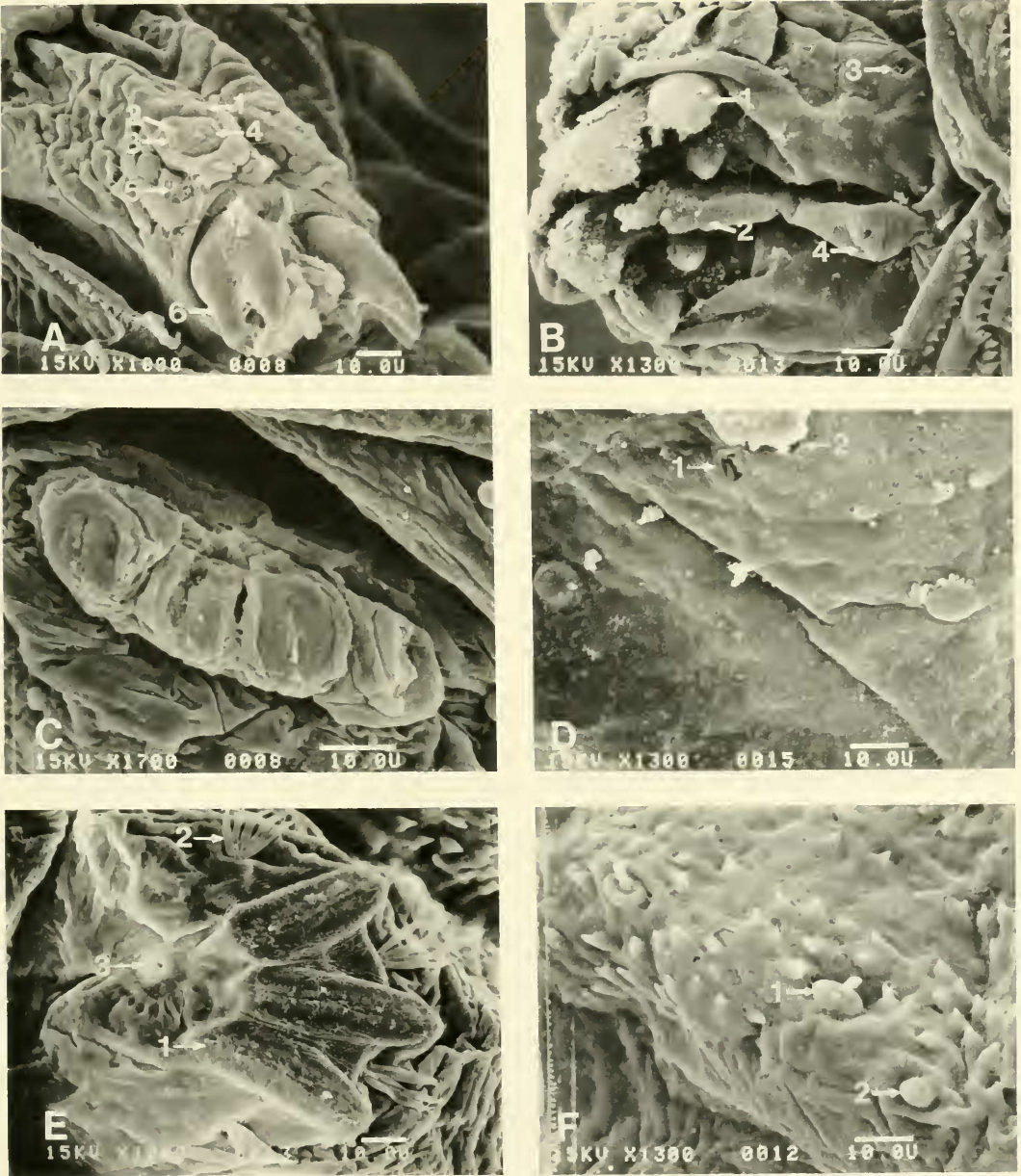


Fig. 2. Third instar larva of *T. arizonaensis*: (A) gnathocephalon, 1—dorsal sensory organ, 2—lateral sensory organ, 3—pit sensory organ, 4—stomal sense organ, 5—median sense organ, 6—mouth hooks; (B) 1—mouth hooks, 2—median oral lobe, 3—ventral sensory organ, 4—labial lobe sensilla; (C) anterior prothoracic spiracle; (D) lateral spiracular complex, first abdominal segment, 1—spiracle, 2—sensilla; (E) posterior spiracular plate (dorsal at top), 1—rima, 2—interspiracular process, 3—median ecdysial scar; (F) caudal segment sensory papillae, 1—stelex sensillum, 2—tuberculate, medusoid chemosensillum.



Fig. 3. Puparium of *T. arizonaensis*: (A) habitus, anterior to the right; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) posterior spiracular plates, 1—rima, 2—spiracular slits, 3—interspiracular processes, 4—compound sensilla.

ber of sensilla may be species-specific (Goeden, Headrick, and Teerink, unpublished data). The median oral lobe is attached to the floor of the mouth lumen, as in *N. viridescens* (Goeden and Headrick 1992). To date, these are the only two Nearctic species of Tephritidae reported to have attached median oral lobes (DHH, unpublished data).

Second instar.—Second instar cylindrical; gnathocephalon cone-shaped and rounded posteriorly; mouth hooks bidentate; median oral lobe similar to that of third instar and attached to floor of mouth lumen.

Most structures were similar in shape and placement to those of the third instar. Quality specimens of all immature stages were difficult to obtain due to the nature of their feeding habits. Early instars were rarely obtained and unsuitable for SEM except for general observations.

Puparium.—Puparium superficially smooth, elongate-ellipsoidal and rounded anteriorly (Fig. 3A); anterior end bears invagination scar (Fig. 3B-1) and raised anterior thoracic spiracles dorsolaterad of the invagination (Fig. 3B-2); posterior spiracular plates bear slightly raised, oval rimae (Fig. 3C-1), with opened slits measuring 0.04 mm in length (Fig. 3C-2); branches of longest interspiracular processes measured 0.01 mm in length (Fig. 3C-3); compound sensilla ventrad of spiracular plates remained intact and erect (Fig. 3C-4).

Because of plant tissues adhering to the puparia (Fig. 3A), only their ends, which were free of debris, could be examined.

DISTRIBUTION AND HOSTS

Jenkins and Turner (1989) described the range of *T. arizonaensis* as "southcentral New Mexico west to southern California and south to northwestern Mexico." The distribution of its only confirmed host plant, *B. sarothroides* (Jenkins and Turner 1989) within this range was described by Boldt et al. (1988) as "common in sand or gravel riparian washes, drainage areas, and low hills

at elevations of 300–1500 m above sea level.”

Jenkins and Turner (1989) recorded *T. arizonaensis* from terminal galls, stem tip mines (first reported by Foote and Blanc 1963), and female flower heads of *B. sarothroides* in Arizona and California. We add the following rearing records for F₂ males and females of *T. arizonaensis* reared from female and male flower heads of *B. sarothroides*, all collected in San Diego Co., CA: Highland Valley, SE of Escondido at 485 m, male heads, 11 Sep 1989, 3 males and 1 female. Barrett Junction at 274 m, female heads, 21 Sep 1989, 1 female. Lake Hodges Dam at 128 m, male heads, 8, 12, 16 Oct 1990, 5 males and 8 females; female heads, same dates, 12 males and 3 females. Del Mar Heights, W of Rancho Penasquitos at 241 m, male heads, 16 and 29 Oct 1990, 1 male; female heads, 8, 12, and 16 Oct 1990, 2 males and 7 females. Rancho Bernardo, NW of Black Mountain at 165 m, male heads, 12, 16, and 22 Oct 1990, 4 males and 8 females.

The host record for *B. pilularis consanguinea* (deCandolle) C. B. Wolf in Wasbauer (1972) remains unconfirmed. This host record is suspect, and may result from host-plant misidentification, as this species is sometimes very difficult to distinguish from *B. sarothroides* (Munz 1974). Similarly, the record for specimens “taken on” *B. sergilloides* Gray reported in Jenkins and Turner (1989) may be a sweep record, as RDG has reared only *Trupanea* spp. from flower heads of this shrub (Cavender and Goeden 1983, Goeden 1985).

BIOLOGY

Egg.—In laboratory cagings, eggs were inserted singly for all or most of their lengths mainly into apical buds, and a few into distal axillary buds on current season’s branches (Fig. 4A). As reported for *T. baccharis* (Goeden and Headrick 1991a), a thin circle of necrotic tissue delimits the oviposition

site. The eggs of *T. arizonaensis* are inserted pedicel-last, downward and at a slight angle to the long axis of a branch. Eggs of the F₂ generation of *T. arizonaensis* presumably also are laid singly in both male and female flower heads of *B. sarothroides*. However, the low densities of this generation relative to the abundance of small flower heads produced in the field during our study period precluded our finding eggs in samples. As observed with other non-frugivorous tephritids, e.g. *T. baccharis* (Goeden and Headrick 1991a), the embryo reversed itself 180° just before eclosion, so that it immediately gained access to the plant tissues within which the egg was inserted. Eggs hatched in about 1 week at insectary temperatures of $27 \pm 1^\circ\text{C}$.

Larva.—The newly hatched larva immediately tunnels into the pith of the branch tip (Fig. 4B). Shortly after molting to the second instar, it discontinued its tunneling, confined further pith feeding to excavating an area sufficient to accommodate its growing size, while mainly feeding on sap that accumulated in the cuplike depression at the base of the mine (Fig. 4C). No obvious tissue proliferation or attendant swelling or elongation of the branch tip occurred, as only the epidermis remained uneaten and was stretched to accommodate larval growth (Fig. 4D); therefore, the width of the mine was as wide as the third instar itself. This branch tip-mining habit is unique among Nearctic tephritids, and among the hierarchy of gall types, it may represent the connecting link in the transition from nongalled flowerheads, i.e. the most primitive type of tephritid stem “gall” lacking in tissue proliferation (Freidberg 1984). The next step in this hierarchy may be branch galls of the type formed by the F₁ larva of *Tephritis stigmatica* (Coquillett), which extends its mine farther basally into the branch pith parenchyma, which then proliferates as callous or wound tissue in reaction to continued larval feeding and excavation to form

a gall (Freidberg 1984, Goeden 1990). Moreover, *T. stigmatica* also infests, but does not gall, the flower heads of its host plant (Goeden 1990). Likewise, the older, F_2 larvae of *T. arizonaensis* deeply score, but do not gall, the receptacle of the flower heads within which they developed singly and largely fed on sap, as reported for larvae of several other genera and species of florivorous tephritids, i.e. Freidberg (1984), Goeden (1988b); Goeden and Headrick (1991b, 1992); Headrick and Goeden (1990a) (Fig. 4E). Thus, the F_1 and F_2 larvae feed similarly, whether mining branch tips or individual flower heads; again, evidence of the primitive nature of these mines in the hierarchy of tephritid gall types (Freidberg 1984). The lengths of 177 branch-tip mines measured from base to branch apex was 6.6 ± 0.1 (range, 3–8.8) mm. The widest width was 1.3 ± 0.1 (range, 1.0–1.8; $n = 138$) mm at the base of the mine. Mines were scattered over the crowns of host plants.

An interesting behavioral adaptation exhibited by *T. arizonaensis* was the cutting of a small (ca. 0.1 mm) hole at the base of the feeding tunnel through the epidermis after the larva had ceased feeding, but before it pupariated. This hole always was present and allowed the larva to reverse itself 180° within its tunnel by serving as a vent to insure that suction pressure would not build and prevent the larvae from turning in the otherwise intact, sap-filled, basal part of its feeding cavity. This vent hole was separate from the exit hole of the adult described below. The larvae invariably pupariated with their heads toward the branch apices. The branch tips distal to the puparia always were killed.

Puparium.—The puparia were glued by dried sap to the cup-like feeding depressions basally and were tightly covered by the uneaten branch epidermis that covered them (Fig. 4F). This epidermal covering proved difficult to remove; consequently, the following measurement of the widths of 166 puparia included the thin, host epidermal cylinder, i.e. 1.6 ± 0.1 (range, 1.2–1.9) mm.

The mean length of 69 puparia was 2.9 ± 0.02 (range, 2.5–3.6) mm. The distance from the base of the mine to the base of the puparium averaged 0.6 ± 0.01 (range, 0.09–1.04) mm. The adult emerged through a flap of host epidermis at the distal end of the larval chamber (Fig. 4G). F_2 flies pupariated in the center of flower heads (Fig. 4H) and emerged outward through the surrounding pappus hairs from fragile cells fabricated of dried, sap-impregnated achene and pappus fragments.

Adult.—*Tephritis arizonaensis* is among the smallest of the California *Tephritis* species. It is rarely collected as an adult, and the early immature stages are even more rarely observed (Foote and Blanc 1963).

General behaviors: Both sexes were observed to groom throughout the day. Grooming took place during resting, feeding, and copulation. The grooming process is typical for tephritids, i.e. the forelegs are used to clean the head and midlegs, and the hindlegs are used to groom the thorax, wings, and abdomen. The distal parts of the fore tibia were used to clean the antennae and mouthparts. There was no detectable sequence to grooming, and except for females in copula, other activities did not influence which body parts were groomed. Adults were most active in the laboratory between 1000 and 1400 h PST, exhibiting spontaneous wing displays either with or without the presence of other individuals, orienting to movement, forming feeding droplets, and grooming.

Wing displays: Both sexes exhibited all of the typical wing displays known for tephritids including hamation, enantion, and asynchronous supination (Headrick and Goeden 1990b, 1991, J. F. Green, DHH, and RDG, unpublished data). There were no wing displays unique to this species. Males have no courtship displays, and thus, no unique wing displays. Both sexes exhibited wing displays when orienting toward moving objects or when startled, and both rested with their wings held flat over their dorsa.

The wing display most often observed for

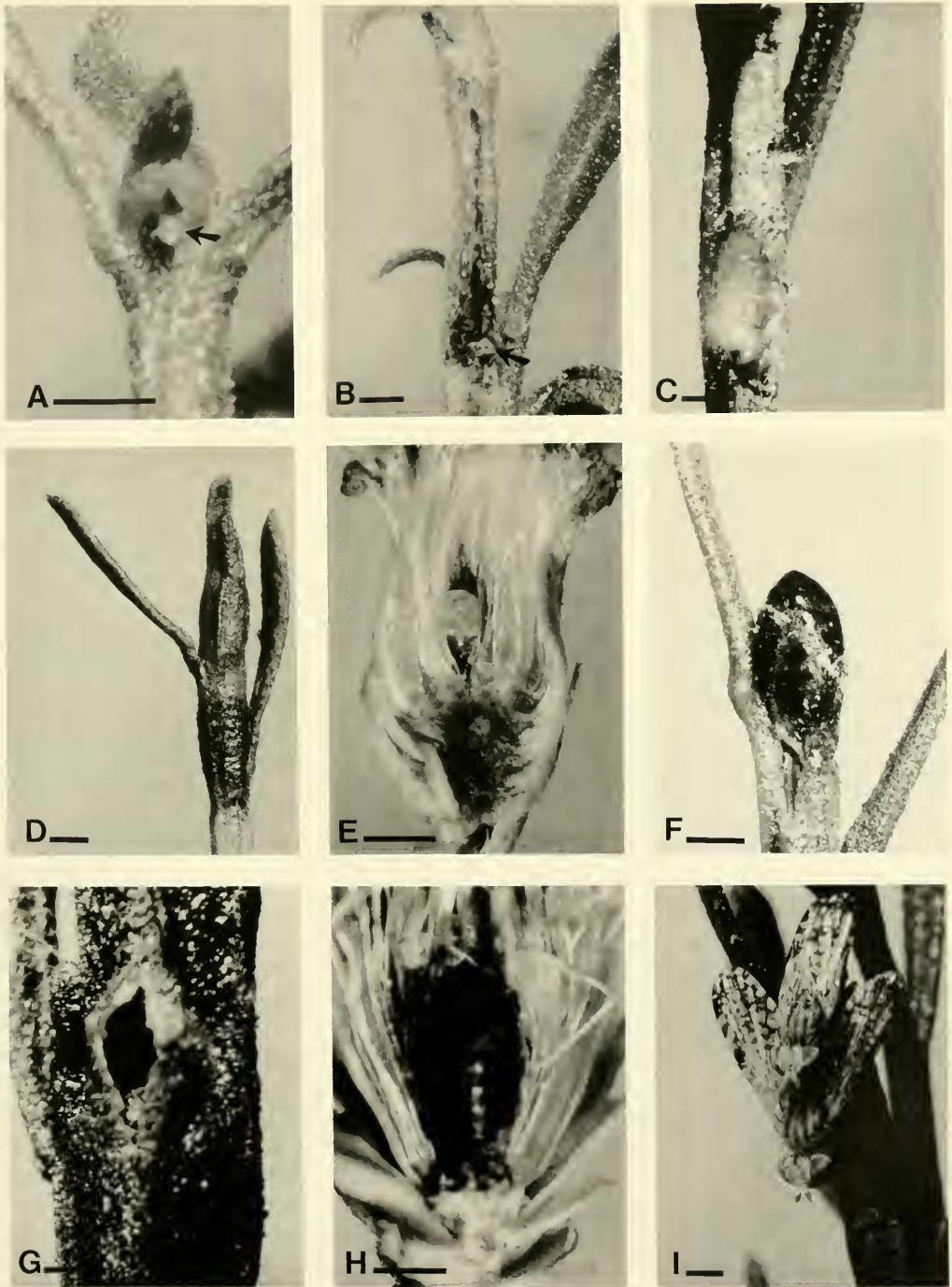


Fig. 4. Life stages of *T. arizonaensis* on *B. sarothroides*: (A) egg inserted in apical bud, (B) second instar in mine at branch apex, (C) last instar exposed, (D) intact branch tip mine, (E) larva in male flower head, (F) empty puparium basally affixed to branch and partly covered by epidermal remnant, (G) exit hole to adult, (H) puparium in male flower head, (I) mating pair.

both sexes was asynchronous supination, as first described for *Trupanea californica* Malloch (Headrick and Goeden 1991). Both sexes displayed asynchronous supinations spontaneously as well as in response to other individuals. The asynchronous supination display was irregular, i.e. one wing was extended more than once, and often held extended for several seconds; or regular, i.e. each wing is extended in turn without pause. Males facing or approaching females often embellished their asynchronous supination display by holding one wing fully extended to 90°, with the other wing held flat over their dorsum, then rotating the extended blade beyond 90° several times. The extended wing was returned and the same motion was repeated with the other wing, and so on.

Females generally were unresponsive to wing displays by males; however, if males moved too closely, the females would jump away. Females did not exhibit any unique wing displays and typically held their wings flat over their dorsa and overlapped. Females displayed aggression by extending both wings forward synchronously to 90° while slightly supinated, e.g. when lunging at an intruder. Males sometimes exhibited synchronous wing extensions without supination, i.e. enation (J. F. Green, DHH, and RDG, unpublished data), when approaching females; this wing display is typical among *Tephritis* spp. males observed to date (Goeden and Headrick 1991a, DHH and RDG, unpublished data). Both wings are extended while slightly supinated from a resting position at ca. 30°, outward to 90°; this behavior often is followed by swaying. Both sexes swayed during wing displays and both exhibited abdominal flexures during asynchronous wing supinations (Headrick and Goeden 1991).

Male-female interactions: Figure 5 is a flow diagram of male-female interactions prior to and including copulation. Each component is discussed and the number of observations is given for each. During peak

activity, there were many encounters between individuals, with approaches initiated by both sexes. Males approached females either passively with their wings flat over their dorsa ($n = 3$), or with wing displays ($n = 26$). Males also visually tracked females while remaining still ($n = 19$), sometimes having to stilt, i.e. rise on their forelegs, to see females as they moved overhead and behind them. Males sometimes exhibited abbreviated wing displays while watching females, i.e. slight supinations to 45°. If a female approached a male, he either sat still, with wings flat over his dorsum, and when she moved away, he remained still ($n = 10$) or decamped upon approach ($n = 11$). Males did not exhibit any of the common tephritid courtship displays in the laboratory, i.e. abdominal pleural distension, wing displays, or mouthpart extension (Headrick and Goeden 1990a, 1991, Goeden and Headrick 1992). However, no field observations were conducted, and such behaviors may only be manifested on the host plant with other adults present (Headrick and Goeden 1990b). Males ready to initiate copulation either stalked a female and attempted to jump on her dorsum or did so without stalking. The process of stalking lasted from a few seconds for a single attempt, to ca. 1 h, during which time males intermittently approached females passively or with wing displays, then turned and moved away. Mounting attempts were not always successful, as females attempted to fly off when males jumped towards them. Males also jumped onto females that passed closely by without any stalking. Thus, males are opportunistic in their attempts to mount females. This opportunistic mating system has evolved several times in different genera of Tephritidae, e.g. *Aciurina* and *Procecidochares*, and is based on the distribution and abundance of the tephritid and the developmental stage of its host plant (DHH, unpublished data). Males that exhibit this mating system have enlarged fore femora for grasping and holding their intended fe-

male partner. The enlarged fore femur is a sexually dimorphic character as reported for *Aciurina trixa* (Coquillett), *Valentibulla dodsoni* Foote (Dodson 1987), and *A. thoracica* (Headrick and Goeden, unpublished data). Measurements of the three leg parameters, hind tibial length (HTL), fore femoral length (FFL), and fore femoral width (FFW) from samples of five males and five females from both F₁ and F₂ populations were analyzed for differences in male femoral size. Female FFW averaged 0.21 ± 0.004 (range, 0.19–0.24) mm; male FFW averaged 0.23 ± 0.005 (range, 0.19–0.24) mm. These means were not statistically different (*t*-statistic = 1.372, $\alpha > 0.05$). The FFL averaged 0.21 ± 0.001 mm for both sexes. Thus, fore femoral size was not sexually dimorphic, because the fore femora were enlarged in both sexes. The middle and hind femora in *T. arizonaensis* are isocylindrical and the fore femora are proximally pyriform. Enlarged fore femora in males of *T. arizonaensis* may provide an advantage in holding potential mates, as confirmed by observing their behavior, but no such use has been elucidated for females.

Copulatory induction behavior and copulation: Males jumped on females to initiate copulation. Once a male mounted a female, he raised her ovipositor ca. 45° with his hindlegs and hind tarsi held flat against her ventrum (Fig. 4I, 6). The male then curled his abdomen under and placed his epanandrium against the ovipositor apex and began rubbing his tarsi against the venter of the female's abdomen and oviscape (Fig. 6A). If the female was receptive, she exerted her aculeus after several seconds and its tip was grasped by the surstyli. When the aculeus entered the surstyli, the male's abdomen was moved backward. He then dropped his hindlegs to the substrate, and the ovipositor was lowered. The aculeus was bent upward slightly to expose the ventral flap, and the eversible membrane expanded as the aedeagus entered the cloaca. The fully exerted aculeus slowly retracted as the ae-

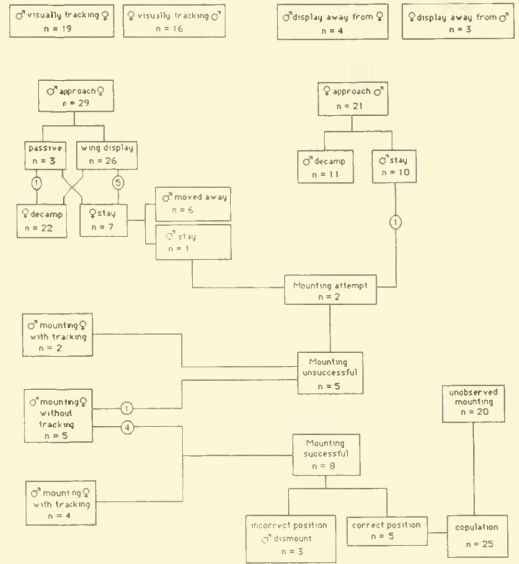


Fig. 5. Flow chart of courtship and copulatory behaviors, with numbers of observations exhibited by *T. arizonaensis* in laboratory arenas.

deagus was further inserted. The final copulatory position is typical for tephritids (Fig. 4I, 6B). The head of the male was positioned over the middle of the female's abdomen and behind her scutellum. His hindlegs wrapped around the apex of her ovipositor when first gaining intromission, and then rested on the substrate. His midlegs grasped the middle of her abdomen, and his forelegs rested on top of her abdomen near the thorax, such that his tarsi were parallel with the midline of her body. The wings of the female were held flat at ca. 45° to each other; the wings of the male were flat over his dorsum and spread slightly such that the costal margins were parallel (Fig. 4I). While in copula, the female intermittently used hydrostatic pressure to exert its aculeus against the male, but the male held its abdomen in place, resulting in the eversible membranes ballooning due to increased pressure. Copulation times in the laboratory averaged 5.5 h (range, 2.5–8 h, n = 25).

Territoriality: Male were not observed to be territorial in the laboratory, and no de-

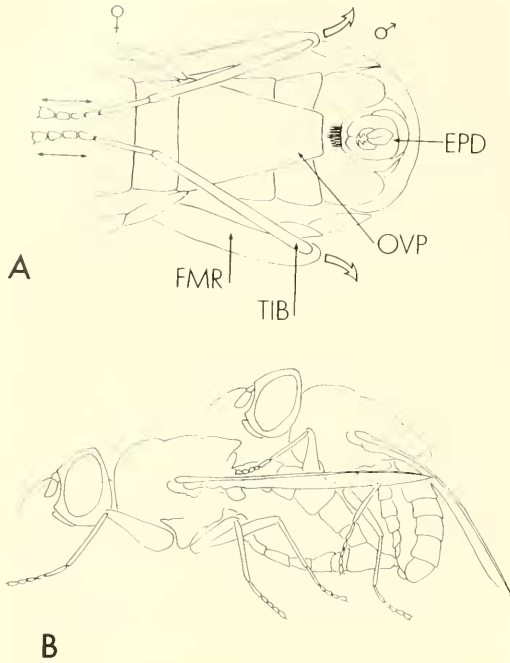


Fig. 6. (A) Ventral view of male mounted on female displaying copulatory induction behavior prior to aedeagus exertion. The hindlegs of the male are bent underneath the abdomen of the female. (B) Side view of final copulatory position after insertion of the aedeagus.

tailed field observations have been made on this species. Other tephritid species that have no male courtship, and opportunistic mounting, e.g. *A. trixa*, usually do not establish or defend territories (Dodson 1987, DHH, unpublished data). However, *T. stigmatica* males, which have no courtship displays and mount females opportunistically, have exhibited highly ritualized territorial displays and combat in laboratory cagings. Therefore, we cannot predict from our laboratory studies whether *T. arizonensis* males are territorial in nature.

Seasonal history. — *Tephritis arizonensis* is bivoltine and synovigenic in southern California. The adults are long-lived, i.e. 13 males lived 165 ± 12.5 days (range, 94–243 days); 13 females, 137 ± 10.0 days (range, 48–199 days) under insectary conditions. Thus, F_2 adults produced in male and fe-

male flower heads of *B. sarothroides* overwinter, probably as dispersed, sexually immature, unmated individuals in proximity to sources of fresh water in sheltered locations, e.g. riparian habitats (Goeden 1987, 1988b, Headrick and Goeden 1990b, Goeden and Headrick 1991a). Following resumption of winter rainfall and host-plant vegetative growth, overwintered adults are attracted to and gather on their host plants for mating, copulation, and oviposition in February–April. Our laboratory matings showed that individuals reared from flower heads never mated and remained reproductively immature while they overwintered; whereas, overwintered adults swept from hosts readily mated under laboratory conditions. The F_1 generation develops as branch-tip miners as described above, and emerges as adults in May to oversummer. Larvae were present in March–April; puparia in April–May. *Baccharis sarothroides* flowers in the fall, i.e. August–October, at which time the F_2 generation develops in heads as described above.

The seasonal variation in color of adults reported by Jenkins and Turner (1989) was confirmed, although as they noted, this tends to be less well defined in *T. arizonaensis* than in some other species of *Tephritis* associated with *Baccharis* spp., e.g. *T. californica* Doane. The F_1 generation comprises the dark morphs; the F_2 generation, the light morphs described by Jenkins and Turner (1989). If this color variation somehow is involved in thermal regulation, e.g. as suggested for dark-winged *Eutreta diana* (Osten-Sacken) (Goeden 1990), intuition suggests that the dark morphs which oversummer instead should be lighter to reduce warming than the light morphs that overwinter! The biological significance of this seasonal color variation described by Jenkins and Turner (1989) should be addressed experimentally.

Natural enemies. — Three species of chalcidoid Hymenoptera adults were reared from *T. arizonaensis* during this study.

Eleven specimens of a *Pteromalus* sp. and two specimens of a *Dinarmus* sp. (Pteromalidae) were reared from F₁ puparia as solitary, primary, endoparasitoids. Two *Eupelmus* sp. (Eupelmidae) were reared from F₁ puparia as solitary, primary parasitoids; another specimen was reared from a flower head (F₂ gen. host), as was a male of an unidentified Torymidae. The above named parasitoids of the F₁ flies also parasitized *A. thoracica* on *B. sarothroides* (Headrick and Goeden, unpublished data).

Biological control.—This tephritid may be worth considering as a candidate agent for biological control of groundsel bush, *Baccharis halimifolia* L., which is native to the Southeastern United States, and an introduced weedy shrub in southern Queensland and northern New South Wales, Australia (McFayden 1978), if it can transfer to this plant species. Several insect species, but no tephritids, have been introduced from North America into Australia for biological control of this toxic rangeland weed (McFayden 1978, Julien 1992). Some of these biological control agents were obtained from other species of *Baccharis*, including *B. pilularis* in California (Julien 1992). Russia also has introduced and established three insect species from North America (two of them via Australia) for the biological control of *B. halimifolia* in recent years (Julien 1992).

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